

SCLEROCARPUS UNISERIALIS (COMPOSITAE) IN TEXAS AND MEXICO

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The genus Sclerocarpus (Compositae-Heliantheae) consists of yellow-rayed sunflowers common locally in southeastern Texas and in much of Mexico and Central America. Of the eight species known, one occurs widely in tropical Africa whereas the others are American. Although one species is perennial the rest are somewhat weedy annuals most commonly encountered along roadsides and field margins or in grainfields and pastures. Superficially, Sclerocarpus resembles several other genera of the Heliantheae. It is unique, however, in that the receptacular bracts completely surround the disk achenes, and at maturity those near the margin of the disk become thick and hard, closely surround the achene, and develop tubercles or swellings on the surface. This peculiar fruit type, consisting of the achene and its closely investing bract, is here designated a sclerocarp.

The genus was proposed by J. N. Jacquin (1781) who published a series of plates including one entitled Sclerocarpus africanus. It represented the African species later validly published under that name. A second species was discovered by Thomas Drummond at San Felipe, Austin County, Texas, and described by Hooker (1837) as Gymnopsis uniserialis. This was later transferred to the proper genus by Hemsley (1881). Correll and Johnston (1970) recognize S. uniserialis as the only species in Texas, and indicate that it is widespread in Mexico. A number of populations closely related to S. uniserialis do occur in Mexico, and recent studies on their morphological variation and geographic range have been the basis of the taxonomic revision of the group presented here.

One population from Mexico was described as S. uniserialis var. papposus Greenman. This differs in so many characters and to such a degree from the Texas plants, however, that it must be regarded as a distinct species. The remaining populations are more closely related, morphologically, to the Texas plants and must be considered as sub-specific elements of S. uniserialis. Thus circumscribed, S. uniserialis is the most variable species in the genus and the most wide-ranging one in America. It consists of three major populations and a number of minor ones, all apparently having the same chromosome number and varying degrees of isolation from each other. These major populations are here treated as varieties and may be distinguished from each other and from S. papposus by the following key.

KEY TO THE TAXA

- A. Involucral bracts inconspicuous, acicular-involute, mostly less than 3 mm. long; receptacle white-pubescent, scarcely enlarged from the peduncle; pappus of marginal disk achenes 1.5-4 mm. long; anthers conspicuously exerted at anthesis.....1. S. papposus
- A. Involucral bracts evident, mostly 4-30 mm. long; receptacle glabrous, conspicuously enlarged from the peduncle; pappus of marginal disk achenes less than 1.5 mm. long; anthers mostly retained in the corolla at anthesis.....2. S. uniserialis
- B. Receptacular bracts green in bud or red only on apical margin; mature marginal sclerocarps ribbed or with low, uniform tubercles; involucral bracts mostly more than 5 mm. long; plants mostly more than 5 dm. tall.
- C. Mature marginal achenes elliptic-fusiform; mature marginal sclerocarps cylindrical-conoid, the body mostly low-tubercled, gradually reduced to the beak, not or scarcely bent.....
.....2a. var. uniserialis
- C. Mature marginal achenes obliquely obovate in lateral outline; mature marginal sclerocarps somewhat laterally compressed, the body smooth or ribbed, the beak strongly bent from it.....
.....2b. var. frutescens
- B. Receptacular bracts red or purplish in bud; mature marginal sclerocarps swollen about the middle with large complex tubercles; involucral bracts mostly less than 5 mm. long; plants mostly less than 5 dm. tall.....2c. var. rubridiscus

TAXONOMY

1. SCLEROCARPUS PAPPUSUS (Greenm.) Fedde, comb. nov.

Sclerocarpus uniserialis var. pappus Greenman, Field Mus. Publ. Bot. 2:346. 1912. Type: MEXICO: GUERRERO: Rio Balsas, 26 Aug 1910. C. R. Orcutt 4208 (Holotype F! Isotype MO!).

Erect, mostly strigose annuals to 1 m. tall, the branches long and slender, opposite below, alternate above; leaves 5-12 (20) cm. long, blades ovate-trullate to deltoid, scabrous to strigose above, strigose beneath, petiole mostly one-fourth to one-third as long as the blade; heads few to several, obconoid, 10-20 mm. high, on long, often curved, peduncles; receptacle green, strigose, conical, 1.5-3.5 mm. high, little wider than the peduncle; involucre inconspicuous, bracts 3-7, green, mostly less than 3 mm. long, involute-acicular in age; ray flowers 3-7, neutral, ligule yellow-orange, mostly broadly ovate, 6-12 mm. long, tube greenish, subequal to the ligule; ray achenes green, fleshy throughout when living, persistent on the receptacle; disk flowers (4) 6-12 (15), arcuate, ascending, corolla 8-14 mm. long, greenish or yellow below, reddish near the lobes, these reddish at the base with the apex recurved, bristly without, papillate within; anthers exerted at anthesis; immature receptacular bracts thin, green, arcuate, tubular, enclosing the corolla nearly to the lobe; mature sclerocarps to 13 mm. long, cylindrical-conoid narrowing gradually to the apex of the achene, more sharply so to the beak or enlarged again about the pappus, the surface with rows of low tubercles; disk achenes fusiform-arcuate, 7-11 mm. long including the pappus, this a conspicuous green or yellow crown of irregular fused bristles to 4 mm. long.

Guerrero, at elevations of approximately 500 to 2,000 meters, flowering August to October.

This species is most closely related to S. uniserialis from which it differs chiefly in its very long pappus, its longer sclerocarps, its very small pubescent receptacle, short involucre bracts, and reduced number of disk flowers. It is a rare species known only from the type collection and two others.

Additional specimens examined: GUERRERO: North of Rio Balsas, Dist. Adama, Temisco, top of Barranca Limo, 30 Oct 1939, Ynez Mexia 8707 (F, GH, MO, NY, US); Taxco Viejo, 18 Sept 1937, R. Q. Abott 402 (GH).

2. SCLEROCARPUS UNISERIALIS (Hook.) Benth. & Hook. f. ex
Hemsley, Biol. Centr. Am. Bot. 2:164. 1881.

Erect, mostly strigose annual, to 2 m. tall, branches long, ascending, opposite below, alternate above, pubescence sometimes somewhat spreading; leaves 3-6 (20) cm. long, the cauline large, long-petioled, soon withering, those of the branches smaller, petiole mostly one-fourth to one-third as long as the blade; blade ovate-trullate to deltoid, scabrous or with ascending hairs above, strigose beneath, margin dentate, apex mostly acute or acuminate, base mostly cuneate; heads few to numerous, hemispheric to cylindric, 7-25 mm. high, solitary, terminating the long-pedunculate branch-ends; receptacle whitish, glabrous, conical, to 10 mm. long; involucre uniseriate, campanulate in bud, spreading or reflexed in age, bracts 5-9 (12) green, mostly 5-10 (15) mm. long, linear-elliptic or oblanceolate, often oblique; ray flowers 5-9, neutral, ligules yellow-orange, ovate-oblong to suborbicular, 6-20 (30) mm. long, the apex shallow-toothed, tube one-fifth to one-half as long as the ligule; ray achenes greenish, fleshy throughout, linear-arcuate when living, shriveled and persistent on the receptacle when dry; disk flowers (5) 15-40 (50), spreading to erect, corolla 6-13 mm. long, gradually enlarged from base to throat, yellow or reddish or with zones of both colors, lobes 2-5 mm. long, recurved, strigose or bristly at the apex without, long papillate near the middle within; anthers mostly retained in the corolla tube; receptacular bracts green or purplish in bud, enclosing the corolla to about the middle, the mature bract (sclerocarp) 3-10.5 mm. long, beaked, green, brownish, purple, or mottled, the surface sparsely strigose, low-ribbed or tubercled, the body often somewhat laterally compressed; marginal disk achenes 3-6 mm. long including the pappus, black, often somewhat laterally compressed, fusiform-arcuate or obliquely obovate in lateral outline; pappus a crown of basally fused bristles sometimes reduced to form one or more scales, mostly less than 1 mm. long.

The total range of S. uniserialis includes an elongated area from southeastern Texas to northwestern Guatemala. The three varieties form a graded series, morphologically, from north to south in respect to the height of the plants, the length of the involucre bracts, the form of the mature receptacular bract (sclerocarp) and other characters. Plants from Texas are 1-2 m. tall with involucre bracts 1-3 cm. long and straight sclerocarps with small tubercles

or none. Plants from Guerrero are typically less than 1/2 m. tall, have involucre bracts less than 1/2 cm. long, sclerocarps which are strongly bent and have large tuberculate swellings about the middle. Plants from eastern Mexico are intermediate in these characters.

2a. SCLEROCARPUS UNISERIALIS (Hook.) Benth. & Hook. f. ex Hemsl. var. UNISERIALIS

Gymnopsis uniserialis Hook., Icones Plantarum, Vol. 2.t.145. 1837. Type: TEXAS: Austin Co., San Felipe, Drummond 135 "bis ...Texas II" (Holotype K!; isotypes GH! K! NY!).

Aldama uniserialis (Hook.) A. Gray, Journ. Boston Soc. Nat. Hist. 6:228. 1850.

Sclerocarpus major Small, Fl. Southeastern U.S. 1250. 1903. Type: TEXAS: Bexar Co., Comale Creek, 1847-1848, Lindheimer 432 (Holotype NY!; isotypes F! GH! MO! NY! US!).

Mostly 1-2 (2.5) m. tall, usually much-branched; leaves 3-6 (17) cm. long, blade ovate-trullate or rhombic, with 3-8 (16) irregular teeth per side; heads few to many, 10-25 mm. high on peduncles to 15 cm. long; receptacle 3-5 (9) mm. long; involucre often strongly reflexed in age, bracts mostly 5-10 (15) mm. long; ray flowers mostly 5-9, 19-20 (35) mm. long, the ligule mostly narrowly ovate; marginal disk flowers inserted nearly perpendicular to the surface of the receptacle; disk corollas yellow or brownish-red; receptacular bracts green or reddish on the distal margin in bud; mature marginal sclerocarps 6-10.5 mm. long, nearly horizontal on the receptacle, the body 1.5-3 mm. diam, long-conoid, narrowing gradually to the beak; the body with a few long longitudinal ribs, sometimes with small rounded tubercles on the ribs or scattered on the beak; mature marginal achenes 4-6 mm. long, narrowly fusiform, slightly oblique, pappus mostly 0.2-0.5 mm. long, usually lengthened adaxially and abaxially, and reduced laterally.

Chromosome number: N = 12 (Feddem 1468, MICH).

The Texas populations of S. uniserialis are well isolated from those in Mexico. Although the species ranges nearly to the Rio Grande at Brownsville, the nearest coastal collections known from Mexico are from southern Tamaulipas. Inland, the nearest Mexican plants of the species have been found near Monterrey. In Texas the species ranges from

Fort Bend County, along the coastal plain to Cameron County, up the Rio Grande to Webb County, and its western limits run through Medina and Bexar Counties to Williamson County. Variety uniserialis is very variable genetically and in response to environmental conditions. J. K. Small described S. major which he differentiated from S. uniserialis on the basis of the larger heads and involucre bracts of the former. Plants of this kind occur widely. The first head to develop terminates the main stem and is usually the largest. It may be especially so early in the season if water is plentiful.

Two distinct color forms of var. uniserialis occur. In most plants the disk flowers, like the rays, are yellow. Most plants from Duval, Kenedy, Brooks, Jim Hogg, Starr, and Willacy Counties, however, have reddish or purplish-brown disk flowers.

2b. SCLEROCARPUS UNISERIALIS (Hook.) Benth. & Hook. f. var. FRUTESCENS (Brandg.) Feddema, comb. nov.

Sclerocarpus frutescens Brandg., Univ. Calif. Publ. Bot. 4:281. 1912. Type: SAN LUIS POTOSI: between Bagre and Minas de San Rafael, Jul 1911, C. A. Purpus 5157 (Holotype UC; isotypes F! GH! MO!).

Long-lived annual, mostly 3-10 dm. tall, sometimes persisting with thickened stem and root and rooting at lower stem and branch nodes; leaves mostly 3-8 cm. long; blade mostly narrowly ovate-trullate, sometimes strigose-pilose beneath, the pubescence sometimes yellowish, margin rarely entire, mostly with 4-6 teeth per side; heads few to several, 8-19 mm. high; receptacle (2) 3-5 (9) mm. long; involucre often reflexed at maturity, bracts mostly 4-8 (13) mm. long; ray flowers mostly 5-7, 9-15 (23) mm. long, the ligule narrowly ovate; disk flowers spreading or ascending, yellow or with a purplish area above the middle, the lobes sometimes with a band of purplish hairs within; receptacular bracts green; mature marginal sclerocarps 5-8 (9) mm. long, with broad body and narrow beak about as long and strongly bent; body of the sclerocarp few-ribbed, 1-2 mm. wide at base, widening above, then narrowing sharply to the tubular beak, rarely with numerous small uniform tubercles; mature marginal achenes 3-4.6 mm. long, considerably oblique in lateral outline, sharply narrowed to the pappus.

Chromosome number: $N = 12$ (Feddema 1502, MICH).

Southeastern Coahuila, Nuevo Leon, southern Tamaulipas, San Luis Potosí, Hidalgo, Guanajuato, Mexico, Veracruz, eastern Oaxaca, Campeche, Yucatan, Quintana Roo, Chiapas, and northeastern Guatemala, at elevations from sea level to 2700 meters, usually flowering from March to September but sometimes persisting into the second season.

This variety is distinguishable from var. uniserialis by its shorter, bent sclerocarps and from var. rubridiscus by the longer involucral bract, green receptacular bracts in bud and sclerocarps which are merely ribbed or with small uniform tubercles.

2c. SCLEROCARPUS UNISERIALIS (Hook.) Benth. & Hook. f. ex Hemsl. var. RUBRIDISCUS Feddema, var. nov.

Plerumque brevis, 2-6 (15) dm. alta; folia (2) 3-4 (9) cm. longa; lamina anguste trullata (2) 3-4 (7) cm. longa; bracteae involucri lineares vel oblanceolatae, circiter 2.5-5 mm. longae, 1-2 mm. latae; receptaculum glabrum; marginis receptaculi paleae maturae valde curvae, 6-8 mm. longae, in medio valde turgido-tuberculatae, corpore rostrum plerumque paullo longiore; pappus 0.3-0.9 mm. longus; achaenia 4-5 mm. longa.

Plants typically 2-5 dm. tall, the lower branches long, the upper 1-3 short; leaves mostly 2-5 cm. long; blade 1-4 (8) toothed, rarely entire or with short basal lobes or rounded apex; heads 9-20 mm. high; receptacle mostly 5-7 (10) mm. long; involucre appressed to the sclerocarps or slightly spreading in age, bracts mostly 2.5-5 mm. long; ray flowers mostly 5-6, ligule ovate or suborbicular, 8-14 mm. long; disk flowers oriented nearly vertically on the receptacle, the corolla 6-12 mm. long, the lobes reddish below, yellow apically with purplish hairs within near the middle; receptacular bracts reddish-purple in bud; mature marginal sclerocarps 5-9 mm. long, with a broad body subequal to the strongly bent narrow beak; body of the sclerocarp 3-4 mm. long, enlarged above with irregular rounded swellings, narrowed sharply to the tubular beak; marginal achenes 4-5 mm. long, somewhat laterally compressed, obliquely obovate in lateral outline.

Chromosome number: $N = 12$ (Feddema 1710, MICH).

Guerrero, Morelos, western Oaxaca, at elevations of 600 to 2,000 meters, flowering July to November.

Type: GUERRERO: 6 mi S. of Chilpancingo, 13 Aug 1961, Feddema 1650 (Holotype MICH).

This variety is distinct in its typical form which occurs in a narrow area of Guerrero from near Iguala to Chilpancingo. It is distinguished by its low stature, the purplish receptacular bracts in bud, the short involucre bracts, and the swollen-tuberculate mature sclerocarps.

In addition to the above major populations of Sclerocarpus uniserialis, there are a number of others related to var. rubridiscus but having various combinations of characters making them somewhat intermediate between this and the other varieties. Most plants from near Taxco and from southern Morelos are taller than the typical Guerrero variety (var. rubridiscus) but those in Michoacan appear intermediate between it and var. uniserialis from Texas. In an elongated area from southern Morelos and Puebla through the Valley of Oaxaca to the Isthmus of Tehuantepec, many populations are found which have some characteristics of var. rubridiscus. These plants constitute a relatively uniform population over a large area and are intermediate in form between var. rubridiscus and var. frutescens.

Chromosome counts for the three varieties of S. uniserialis and for intermediates between var. rubridiscus and var. uniserialis and between var. rubridiscus and var. frutescens indicate that $N = 12$ for all populations. No counts have been made for S. papposus but other species were counted at $N = 11, 14,$ and 18 . The existence of intermediates between the principal populations of S. uniserialis, and their similar morphology and the same chromosome numbers suggests that they are closely related and interfertile. The variation and distribution of the various populations of S. uniserialis and S. papposus suggest a classic pattern of speciation in which an ancestral population, relatively homogeneous and interbreeding, by isolation and migration, develops variant populations. Variation has progressed rapidly and to a high degree in S. papposus. S. uniserialis var. uniserialis, apparently not at present interbreeding with other populations, includes considerable variation within itself. Var. frutescens and var. rubridiscus, well differentiated in parts of their ranges, have intermediates between them. These may be relict populations from a period when differentiation was less advanced or may be the result of more recent hybridization and introgression after differentiation and a degree of isolation.

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